Why do Ant Species Occur in the Matrix and Not in the Forests? Invasion from Other Habitats or Expansion from Forest Gaps (Hymenoptera: Formicidae)

by

Marcelo S. Madureira[1], Tathiana G. Sobrinho[2] & José H. Schoereder[2,3]

ABSTRACT

In a fragmented Brazilian landscape, 24 species of ant, which are considered to be open-area specialists, occur exclusively in the pasture areas around the forest remnant (matrix). In this paper, we propose possible theoretical explanations for the occurrence of these exclusively matrix species, and suggest that these species originally occurred in forest gaps. We also determine whether these species occur in another type of open vegetation, the cerrado (Brazilian savanna). Ants were collected from ten forest gaps within three forest remnants. Ant species sampled in forest gaps were compared to ant species collected from the cerrado. The aim here was to determine whether there were any similarities between the two sets of species, and also to collect information about the origin of matrix ant species. In the forest gaps, we sampled 44 species of ant. Of these, 11 species were also found to occur in matrix areas and eight species in the cerrado vegetation. Two scenarios could explain this result: (I) exotic ant species of open biomes migrate to, and establish in, the matrix; or (II) the species that currently occur exclusively in the matrix areas are originally from forest gaps and have increased their distribution following the fragmentation event. We discuss reasons to support these scenarios as well as their implications for other ecological and conservation processes.

Keywords: Disturbance, Formicidae, Habitat Fragmentation, Invasion, Landscape ecology.

[1] Departamento de Entomologia, Universidade Federal de Viçosa, Viçosa-MG, CEP 36570-000 Brazil.
[2] Departamento de Biologia Geral, Universidade Federal de Viçosa, Viçosa-MG, CEP 36570-000 Brazil.
[3] Corresponding author mail: jschoere@ufv.br

INTRODUCTION

Habitat fragmentation is the loss of continuous habitats, resulting in the formation of one or several smaller and isolated remnants (Lovejoy *et al.* 1986, DeSouza *et al.* 2001, Laurance 2008), surrounded by matrix habitats (i.e. pastures, crops and plantation), which can strongly influence the connectivity between fragment (Turner 1996, Didham 1997, Ricketts 2001, Sobrinho *et al.* 2003). Fragmentation is considered to be one of the main processes responsible for the loss of biodiversity in tropical ecosystems (Didham *et al.* 1996, Turner & Corlett 1996, Majer *et al.* 1997, Davies & Margules 1998, Vasconcelos & Delabie 2000) and, therefore, has been frequently studied over the past few decades.

Fragmentation affects biodiversity and species composition through several processes, such as area reduction (DeSouza & Brown 1994, Carvalho & Vasconcelos 1999) and an increase in isolation among remnants (Hanski *et al.* 1994, Ricketts *et al.* 2001), as well as through secondary effects, such as edge and shape effects (Murcia 1995, Sobrinho & Schoereder 2007) and invasion by exotic species from the surrounding matrix (Sobrinho *et al.* 2003, Schmidt *et al.* 2008).

The creation of edges between remnants and matrix areas can lead to changes in species number, population abundance and species composition (Murcia 1995, Zheng & Chen 2000, Sobrinho & Schoereder 2007), because it increases the ration between perimeter and area (DeSouza *et al.* 2001), consequently increasing the proportion of habitats exposed to the matrix (Kapos *et al.* 1997). Edge creation causes microclimatic changes, increasing the incidence of winds and solar radiation and reducing the humidity in the strip that extends from the edge until approximately 100 m into the core (Lovejoy *et al.* 1986, Laurance & Yensen 1991, Murcia 1995, Laurance 1997, Turton & Freiburger 1997). In this way, edge creation can cause alterations in communities of several animal taxa, including birds, mammals and invertebrates (Lovejoy *et al.* 1986, Fowler *et al.* 1993, Brown & Hutchings 1997, Didham 1997, Didham *et al.* 1998) and specifically ants (Sobrinho & Schoereder 2007).

The influence of edge creation on communities depends on the type of matrix (Laurence 2008), because this habitat type can influence fragment connectivity (Ricketts 2001, Donald & Evans 2006, Laurence 2008). Matrices

that are significantly different from the pristine vegetation and microclimate tend to be more hostile for native species (Sodhi *et al.* 2005), decreasing their permeability into such areas. Therefore, the matrix type can influence the nature and magnitude of edge effects in forest fragments (Laurance 2008).

Some researchers report the existence of typical animal species in open areas (Hölldobler & Wilson 1990), which are adapted to drier and sunnier environments, in contrast to the humid and dark core remnant (Harper *et al.* 2005). Therefore, it is expected that fauna specialists will exist in matrix areas and that these species will also be present in edge habitats. In addition, these species might also occur more frequently in small remnants, which are more affected by edge effects (Sobrinho & Schoereder 2007). By contrast, typical open-area species might also occur in gaps in the remnant core independently of remnant area, although this pattern has not yet been investigated.

In the fragmented landscape in the Viçosa region, southeastern Brazil, several studies have been carried out to verify the effects of habitat fragmentation on ant communities. In these studies, ant diversity and composition has responded to area, isolation, edge, shape and matrix effects (Sobrinho *et al.* 2003, Schoereder *et al.* 2004a, Schoereder *et al.* 2004b, Ribas *et al.* 2005, Sobrinho & Schoereder 2007). However, as these papers did not sample from forest gaps, the effect of such environments on the composition and diversity of ant species within this landscape remains unknown.

In the above-described landscape, ants were sampled for three consecutive years from 18 remnants. In ten pasture matrix locations surrounding the remnants, ants were sampled during one of these years. Although the remnants had been sampled more exhaustively than had the matrix pastures, Sobrinho *et al.* (2003) reported the occurrence of 24 ant species that occurred exclusively in the matrix, and these were considered to be open-area specialists.

In the current paper, we propose possible theoretical explanations for the occurrence of exclusive ant species in matrix pastures surrounding forest remnants in the Viçosa region. We hypothesize that these species also occur in forest gaps and also verify whether these species occur in other open vegetation types, such as the cerrado (Brazilian savanna). These hypotheses might also apply to other areas that have undergone fragmentation, because they propose explanations of the changes in not only species richness, but also species composition.

METHODS

Study area

The study was carried out in the Viçosa region, southeastern Brazil (20° 45' S, 42° 50'W). This region was covered by forest up until the 20th century, when an accelerated process of fragmentation began. The pristine forest was fragmented and intermingled with pastures and coffee plantations mainly during the 1930s and 1940s (Gomes 1975). The remaining forest vegetation has been restricted to a few patches, particularly on hilltops. From the 1960s onwards, agriculture diminished in the region and several forest areas regenerated into secondary forests. Currently, there is a mosaic of forest remnants in the region, with areas varying from three to 300 ha, forming an ideal system to study the effects of fragmentation. In addition, there is a large amount of available information about the species richness and composition of the fragments and matrix.

Sampling procedure

To collect the ant species, ten forest gaps were sampled in the three largest forest remnants chosen based on the 'nestedness' observed in the species distribution in these remnants (personal observation). The larger remnants have more species than the smaller ones (MacArthur & Wilson 1967, DeSouza & Brown 1994) and have most of the species that are also found in the smaller fragments. Therefore, the larger remnants are the best representatives of species richness and composition in the study area. Three gaps were sampled in each of the first two fragments (areas), whereas in the third largest remnant (300 ha), four gaps were sampled. To collect ants, five pitfall traps were placed in the centre of each gap. The pitfall traps were plastic containers (diameter 20 cm, height 15 cm), with an inner chamber containing the bait, in this case honey and sardine. The ants attracted to the bait fell into the pitfall and died in a 70% alcoholic solution. After 48 h, the solution was removed and the ants were taken to the laboratory.

The collected ants were sorted, mounted and identified to genera using identification keys (Bolton 1994). Some species of ants were identified by comparison with the collection of the Laboratório de Ecologia de Comunidades of the Universidade Federal de Viçosa, where voucher specimens were deposited.

The species collected in former studies (Sobrinho *et al.* 2003, Schoereder *et al.* 2004a, Schoereder *et al.* 2004b, Ribas *et al.* 2005, Sobrinho & Schoereder 2007) in the same region were classified into three groups: (i) exclusively matrix species; (ii) exclusively forest species; and (iii) species common to both the matrix and the forest. In addition, data regarding the occurrence of ant species in another vegetation type, the cerrado, were also obtained (Serra do Cipó and Paraopeba; Ribas *et al.* 2003). This vegetation is an open vegetation type that occurs approximately 200 km from the forests sampled.

The ant species sampled in forest gaps were compared to the above lists, to determine whether there were any similarities among them, as well as information about the origin of the matrix species.

RESULTS

The results presented here might not conform to some of those from previous studies in the same region, because the collection underwent a thorough revision by an ant specialist, who split some species and grouped others.

We sampled 44 ant species from the ten forest gaps in the three remnants (Table 1). The revision of the list reported by Sobrinho *et al.* (2003) resulted in 48 ant species in the matrices sampled. After our sampling, 10 of these 48 species remained exclusive to the matrix, as they were not found in any other vegetation sample (Table 2). In addition, five species occurred only in cerrado vegetation and matrix (*Camponotus genatus*, *Cephalotes minutus*, *Pheidole* sp. 7, *Pogonomyrmex naegeli* and *Pseudomyrmex tenuis*), and two only in forest gaps and matrix (*Apterostigma* gr. *Pilosum* sp. 1 and *Crematogaster* sp. 6) (Fig. 1). As we did not consider species that occurred either only in cerrado or in all three habitats (cerrado, forest gaps and matrix), these data were not included.

DISCUSSION

We propose two possible explanations of our result: (I) exotic ant species of open biomes have migrated and established in the Viçosa region; and/or (II) the species that now occur exclusively in the matrix areas were originally from forest gaps and increased their distribution following fragmentation.

The forest fragmentation in the studied region might have enabled inva-

Table 1. Ant species collected in ten forest gaps in three forest remnants in the Viçosa region, Brazil.

Subfamily	Species
Dolichoderinae	*Azteca* sp. 3
	Linepithema sp. 5
Ecitoninae	*Nomamyrmex* sp. 1
Ectatomminae	*Ectatomma edentatum*
Formicinae	*Brachymyrmex* pr. *depilis*
	Camponotus arboreus
	Camponotus atriceps
	Camponotus balzani
	Camponotus cingulatus
	Camponotus crassus
	Camponotus melanoticus
	Camponotus. novogranadensis
	Camponotus rufipes
	Camponotus sp. 2
	Camponotus (Tanaemyrmex) sp. 7
	Camponotus sp. 10
	Myrmelachista sp. 1
Myrmicinae	*Acromyrmex landolti landolti*
	Acromyrmex rugosus rugosus
	Apterostigma gr. *Pilosum* sp. 1
	Atta sexdens rubropilosa
	Crematogaster sp. 3
Myrmicinae (cont.)	*Crematogaster* sp. 4
	Crematogaster sp. 6
	Megalomyrmex goeldii
	Megalomyrmex iheringi
	Pheidole sp. 13
	Pheidole sp. 17
	Pheidole sp. 20
	Pheidole sp. 24
	Pheidole sp. 25
	Pheidole sp. 40
	Solenopsis sp. 1
	Solenopsis sp. 2
	Solenopsis sp. 5
	Trachymyrmex sp.1
	Trachymyrmex sp. 2
	Wasmannia sp. 1
	Wasmannia sp. 2
Ponerinae	*Odontomachus chelifer*
	Pachycondyla lenis
	Pachycondyla magnifica
	Pachycondyla striata
Pseudomyrmecinae	*Pseudomyrmex* sp. 1

sion by exotic ant species from open biomes, such as the cerrado. This disturbance has created vegetation types that are structurally similar to the cerrado vegetation, such as open fields and pastures. Therefore, after fragmentation, species from cerrado might have invaded the Viçosa region. This hypothesized migration can explain the existence of those matrix species that were found in both the matrix and the cerrado, but not in the remnants.

The above scenario can lead to two further developments: the invading

Table 2. Ant species collected in the matrix of the Viçosa region, Brazil. Asterisks represent exclusive matrix ant species, which were not found in forest remnants, forest gaps or cerrado vegetation (Paraopeba e Santana do Riacho-MG).

Matrix ant species	Forest	Gaps	Cerrado
Dolichoderinae			
Linepithema sp. 2	X		
Ecitoninae			
Labidus praedator	X		X
Formicinae			
Brachymyrmex prox. *depilis*	X	X	X
Brachymyrmex prox. *coactus**			
Camponotus cingulatus	X	X	
Camponotus rufipes	X	X	X
Camponotus novogranadensis	X	X	X
Camponotus melanoticus	X	X	X
Camponotus genatus			X
Camponotus crassus	X	X	X
Nylanderia pr. fulva	X		
Paratrechina sp. 2*			
Myrmicinae			
Apterostigma gr. *Pilosum* sp. 1		X	
Atta sexdens rubropilosa	X		
*Cardiocondyla emeryi**			
Cephalotes minutus			X
*Crematogaster abstinens**			
*Crematogaster evallans**			
Crematogaster sp. 6		X	
Cyphomyrmex transversus	X		
Mycetarotes sp. 2*			
*Mycocepurus goeldii**			
Mycocepurus smithii	X		
Trachymyrmex sp. 3	X		
Trachymyrmex sp. 4	X		
Wasmannia auropunctata	X		
Pheidole sp. 1	X		

Table 2 (continued). Ant species collected in the matrix of the Viçosa region, Brazil. Asterisks represent exclusive matrix ant species, which were not found in forest remnants, forest gaps or cerrado vegetation (Paraopeba e Santana do Riacho-MG).

Matrix ant species	Forest	Gaps	Cerrado
Pheidole sp. 2	X		
Pheidole sp. 3	X		
Pheidole sp. 4*			
*Pheidole brevicona**			
Pheidole sp. 6	X		
Pheidole sp. 7			X
Pheidole gr. *flavens* sp. 8	X		
Pheidole sp. 9	X		
Pheidole sp. 10	X		
Pogonomyrmex naegeli			X
Solenopsis saevissima	X		
Ectatomminae			
Ectatomma bruneum	X		X
Ectatomma edentatum	X	X	X
Ectatomma permagnum	X		X
Ponerinae			
Anochetus diegensis	X		
Odontomachus chelifer	X	X	X
*Odontomachus haematodus**			
Pachycondyla harpax	X		
Pachycondyla marginata	X		
Pachycondyla striata	X	X	X
Pseudomyrmecinae			
Pseudomyrmex tenuis			X

ant species might (I) remain restricted to the matrix or (II) invade the matrix and subsequently migrate to the forest gap.

The environmental structure and composition, as well as their temporal modification, affect the distribution, abundance, composition and dynamics of species. Habitat fragmentation can facilitate the establishment of exotic species and modifications of the vegetation, soil and humidity can guarantee the dispersal of these species in an altered environment (Suarez *et al.* 1998).

The fragmentation of ecosystems can decrease population densities, causing local extinctions and leading to a reduction of negative interactions (DeSouza *et al.* 2001). This process can increase the invasibility and establishment by exotic species. In our study region, formation of matrix (pastures) can facilitate the establishment of exotic species because solar radiation, humidity and vegetation are similar to the supposed source habitats of such species. Therefore, it is possible that invader ants in the matrix established in the forest gap of the studied remnant, in a similar way that Argentine ants are able to invade matrix and remnant forest in the USA (Suarez *et al.* 1998). By contrast, in fragmented Amazonian landscapes, where the matrix is also formed by pastures, Gascon *et al.* (1999) found that approximately 24 species (19% of the total) occur exclusively in matrix but that these species did not invade forest remnants.

If invasion really occurs, it might represent a problem to conservation strategies. In addition, the invasion could lead to an increase in competition between native and alien ant species and, if the latter are more competitive, they could exclude native species. The exclusion of native species might have direct

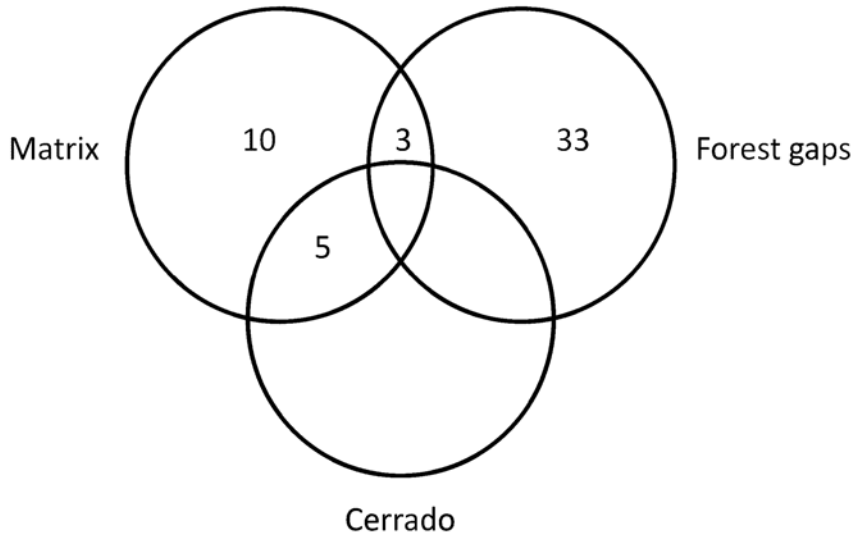

Figure 1.: Venn diagram representing the occurrence of sampled species in the studied environments.

or indirect consequences for other species, given that ants generally maintain several ecological interactions with various organisms. For example, Human & Gordon (1996) showed that, since it invaded the USA, the argentine ant *Linepithema humile* has competitively excluded several native ant species.

In relation to the two species in that occur in both forest gaps and matrix pastures, we suggest that these species were already present in forest gaps of pristine forests in Viçosa. Therefore, the fragmentation event was equivalent to an increase in forest gap areas that facilitated the increase in population size and distribution of these typical gap species in the matrix. Evidence in support of (or against) this hypothesis could be obtained by analyzing the regional distribution of these species. Further studies would be important to clarify the composition ant species of open areas near to Viçosa. If the exclusively matrix species do not exist in such areas, one can assume that these species are endemic to Viçosa. This endemism would be supporting evidence for the hypothesis that species exclusively found in the matrix already occurred in pristine forest gaps and then invaded the matrix.

An unexpected result was that there was no overlap in species sampled from forest gaps and cerrado vegetation (Fig. 1). It might be that both invasion and migration of gap species occurred simultaneously after the fragmentation. Therefore, some species would have come from forest gaps and invaded the matrix, and others would have come from open vegetation, such as cerrado, and migrated to the matrix of the Viçosa region. This process might be continuous as there is no evidence to suggest that it has come to an end.

Finally, it is vital to stress the importance of knowing not only the species richness, but also the community composition of a habitat, because different ant species may indicate what ecological processes occur after habitat fragmentation. Therefore, the species composition might be more important from a conservation point of view.

ACKNOWLEDGMENTS

We are indebted to Carlos F. Sperber for comments on the first draft of the manuscript, and to Fredson Vieira e Silva, who helped us during the sampling. The authors were supported by CNPq grants, and FAPEMIG gave support for the project.

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